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GEOGRAPHIC DISTRIBUTION OF ISOETES SACCHARATA.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY.
LI.

GEORGE HARRISON SHULL.

(WITH MAP)

WHILE making a study of the aquatic vegetation of Chesapeake Bay for the U. S. Bureau of Plant Industry during the summer of 1902, I located several new stations for *Isoetes saccharata* Engelm. This species has had an interesting history, and as our knowledge of its range has greatly increased within the last few years, I have thought it desirable to publish the accompanying map showing the exact distribution as now known, to give a detailed account of its history, and to discuss briefly several problems which have presented themselves for solution.

For a quarter of a century *Isoetes saccharata* Engelm. was known only from its type locality on the Wicomico River and from the Nanticoke, which empty into the bay by a common mouth opposite and a little north of the mouth of the Potomac. Far up the Wicomico, about a mile below the town of Salisbury, Maryland, the plant was first discovered by William M. Canby in 1863. The material was submitted to Dr. Engelmann, who was at that time the highest American authority on the genus, and was first described by him in Gray's *Manual*, 5th edition, p. 676, 1867. In 1874 Canby found a second station at Seaford, Del. Not until 1888 was it collected at a third station, when it was found by Vasey and Coville near Alexandria, Va., in Hunting Creek, a tributary to the Potomac. The material obtained here was not recognized for some years as identical with Canby's material, and was referred by Theo. Holm to *Isoetes riparia* Engelm.¹ The next year Coville found it at Mount Vernon on the Potomac, but this collection seems to have been overlooked

¹ Proc. Biol. Soc. Washington 7:132. 8 Ap 1892.

by Holm, and was not published until in 1900, when it was mentioned in the *Sixth List of Additions to the Flora of Washington*.²

Not until 1893 were specimens recognized as *Isoetes saccharata* Engelm. secured away from Canby's stations on the Wicomico and Nanticoke Rivers. In this year T. Chalkley Palmer discovered it near the western end of the Delaware and Chesapeake Canal in Back Creek, a tributary to Elk River, nearly 140^{km} north of the type locality. During the next two years he discovered it at several other points in both Elk and Sassafras Rivers. These collections formed the subject of an interesting account published in the BOTANICAL GAZETTE in 1896.³

The only new stations which have been published since Palmer's account are given in the *Sixth List of Additions to the Flora of Washington*,⁴ where, besides the reference to Coville's Mount Vernon station above mentioned, two new localities are recorded for the upper Potomac. Along with the publication of these stations were given the descriptions of two new varieties: var. *Palmeri* A. A. Eaton, based upon Palmer's material from Lloyds Creek, Sassafras River; and var. *reticulata* A. A. Eaton, based upon several collections, including that of Vasey and Coville (1888) from the Hunting Creek station, Alexandria, Va.

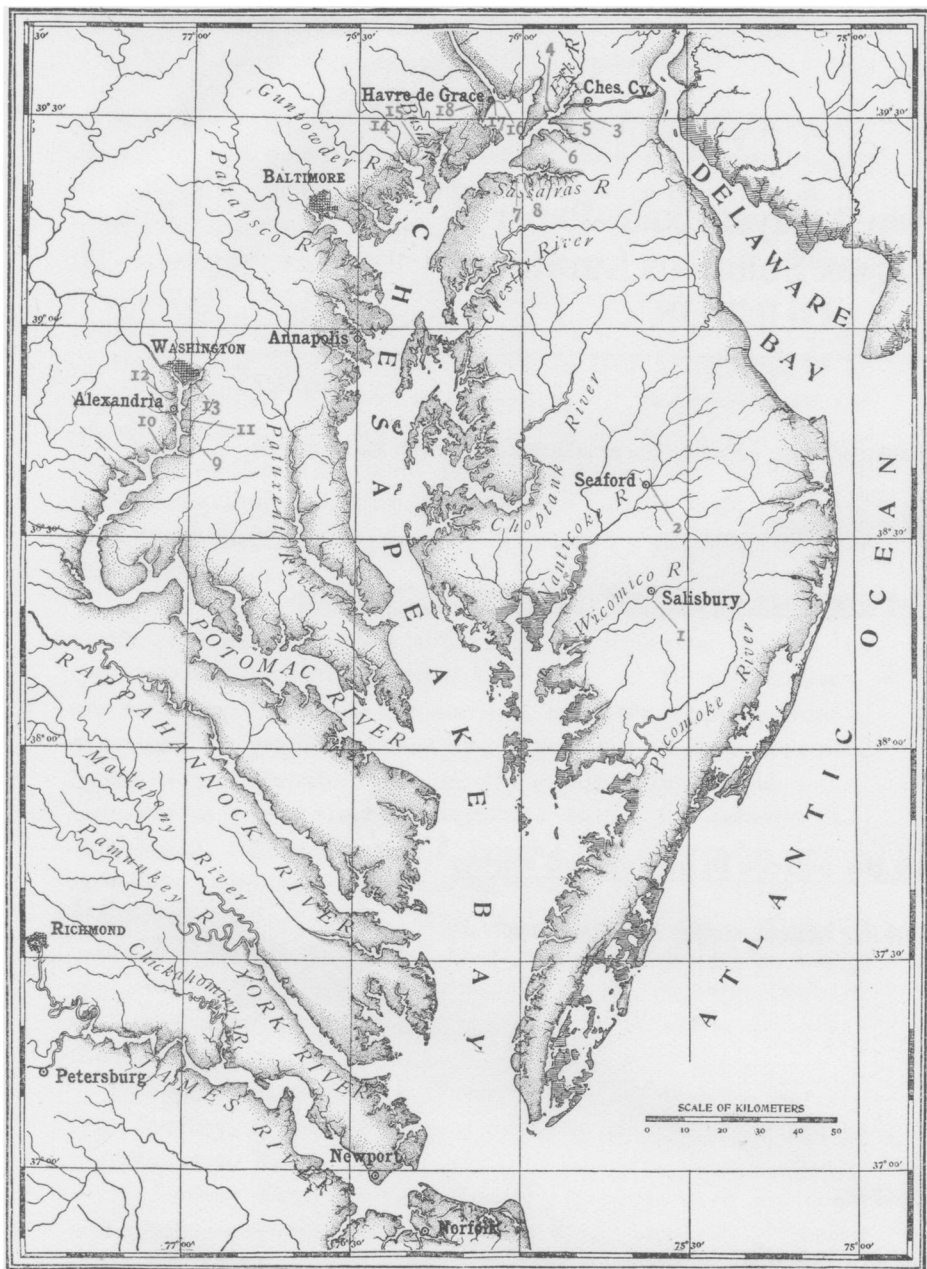
Since the publication of Palmer's paper on *Isoetes*, that collector has located several new stations which are here published for the first time. The most notable of these, and the only one outside of the Elk and Sassafras Rivers, is about 25^m north of the Havre de Grace light at the mouth of the Susquehanna River, and therefore at the very head of the bay.

I believe these are all the localities known for the species before my collections of the past summer. My work was limited almost entirely to the west side of the bay, and my collections of *Isoetes saccharata* were made in the western tributaries and along the shore of the northern part of the bay, my most northern station being only 500^m from Palmer's Havre de Grace station, thus making the circuit about the head of the bay virtually complete.

² Proc. Biol. Soc. Washington 14:49. 19 Je 1901.

³ BOT. GAZ. 21: 218-223. 1896.

⁴ *Loc. cit.*



EXPLANATION OF MAP OF CHESAPEAKE BAY.—Adapted from Coast Chart number 376 of U. S. Coast and Geodetic Survey, and McGee's Drainage Map of the Middle Atlantic Slope (U. S. Geol. Survey, Seventh Annual Report, *pl. 57.*) Stations for *Isoetes saccharata* Engelm. are located at the points in which the index lines cut the shore lines.

So far as could be determined, the index lines are perpendicular to the portion of the shore occupied by the *Isoetes*.

It will be seen then that within the last ten years *Isoetes saccharata* and its forms have been traced from its original station completely to the head of the bay. Wicomico River is yet the most southern station known, but it is not improbable that a careful exploration will result in its discovery in the fresh-water estuarine portions of the more southern tributaries of the bay.

For the sake of completeness and to facilitate further study of the several colonies now known, as well as to serve as an index to the map, I insert the following list comprising all the known stations, with such data as I have been able to gather regarding each. The figure preceding each name agrees with the corresponding station as indicated on the map. In each case the station is at the point in which the index line intersects the shore line.

1. *Salisbury, Md.*—On a label in the herbarium of G. Engelmann, St. Louis, Mo., now in the Missouri Botanical Garden, the type locality is described thus:⁵ “Shores of Wicomico River, one mile [1.6^{km}] below the town of Salisbury, eastern shore of Maryland, on gravel, covered by a thin layer of mud deposited by the tide; alternately covered and exposed by the tide. . . . Growing in the society of *Sagittaria pusilla* (*S. subulata* [L.] Buchenau), *Tillaea simplex* (*T. aquatica* L.), *Hemianthus micranthemoides* (*Micranthemum micranthemoides* [Nutt.] Wettst.) etc.; first found Sept. 15, 1863. Wm. M. Canby.” This label, which bears the date September 8, 1866, evidently belongs to a type specimen. In a letter to the writer, Canby explains that the original station is a sandy or gravelly slope on the south side of the river.

In September 1895 T. C. Palmer, in an attempt to visit the type locality, found the species growing at Williams Point on the Wicomico River.

2. *Seaford, Del.*, is situated at the confluence of the north and south branches of the Nanticoke River, and only 5^{km} below the head of tide water. A label in the Engelmann herbarium,

⁵ A similar but somewhat ambiguous description of the type locality occurs in Engelmann's paper on “The Genus *Isoetes* in North America.” Trans. St. Louis Acad. Sci. 4: 382. 1882.

belonging to one of the original specimens from this station reads: "Muddy and gravelly shores of Nanticoke River near Seaford, Delaware. Wm. M. Canby, Wilmington, Del., August 1874." That this was the first collection at this station is shown by the fact that duplicates in the U. S. National Herbarium and in the Herbarium of the Field Columbian Museum bear the statement that it is "a new station." The area occupied by *Isoetes* at this place is located "nearly opposite the town, a little above it, in fact. The space there is not very large, perhaps 100^{ft}"⁶ (30^m).

3. *Back Creek*, tributary to Elk River, eastern shore of Maryland. This station is on the south shore of the creek about 3^{km} from the western end of Chesapeake and Delaware Canal and nearly 1^{km} below Chesapeake City. The first collection was made by T. C. Palmer in August 1893. He made further collections the following year and published a short statement in the BOTANICAL GAZETTE.⁷

4. *Piney Creek Cove* is a broad indentation in the north shore of Elk River 9–11^{km} from its mouth. On August 13, 1894, T. C. Palmer collected *Isoetes saccharata*, just below the mouth of the small stream which empties at the northeast angle of the cove. This station was also mentioned with the last in the BOTANICAL GAZETTE.

5. *Town Point* is the upper angle formed by the confluence of Bohemia River with Elk River, into which it flows from the east. About 500^m north of this point *Isoetes* was collected on July 31, 1896, by T. C. Palmer. A specimen from this collection in the National Herbarium gives the habitat: "Tidal tract; gravel nearly bare." This station has not been previously recorded.

6. *Cabin Johns Creek* empties into Elk River from the southeast about 5^{km} above the mouth of the latter. A specimen in the National Herbarium bears the data: "July 21, 1896. Cabin John's Creek, Elk River. Tidal tract; gravel covered with mud. Collector T. Chalkley Palmer." This collection has not been published heretofore.

7. *Lloyds Creek* is a large shallow cove on the south shore of

⁶William M. Canby, in a letter.

⁷BOT. GAZ. 20: 32. 1895.

the Sassafras River, about 6^{km} east of Howells Point, and is nearly cut off from the river by a sand spit. On the south shore of this shallow bay, almost due south of its mouth, a very interesting collection of *Isoetes* was made by T. C. Palmer, August 12, 1895. The habitat as described on a label in the National Herbarium is characterized by "reddish sand capped lightly with mud." The material departed in a marked degree from typical *I. saccharata* Engelm., as was pointed out in the collector's interesting contribution in the BOTANICAL GAZETTE in 1896 (*l. c.*). In 1900, A. A. Eaton made this material the basis of his new variety *I. saccharata Palmeri*. In a letter to the writer, Palmer states that at none of his other stations does the *Isoetes* grow in such abundance as at Lloyds Creek.

8. *Turners Creek* empties into Sassafras River from the south about 4^{km} east of Lloyds Creek. On the south shore of Sassafras River just below the mouth of Turners Creek, a station, published here for the first time, was located by T. C. Palmer, July 18, 1897.

9. *Hunting Creek* empties into the Potomac River from the west immediately south of the city of Alexandria, Va. The highway from Alexandria to Mount Vernon is graded for some distance into the shallow part of the creek from each side, and crosses the middle part by a long bridge. The original station is a gravelly bed near the bridge on the right side of the embankment as the bridge is approached from the Alexandria end. The first collection at this place was made by George Vasey and F. V. Coville, July 22, 1888. It has been visited several times since, a recorded visit⁸ having been made by W. R. Maxon, September 22, 1900. Maxon also collected at this station, September 7, 1901, a specimen of this date being placed in the National Herbarium. The writer secured specimens from the same place August 11, 1902, and also found it on the same side of the embankment which leads from the opposite end of the bridge toward Mount Vernon. These areas are not large, but the material is fairly abundant. The soil consists of pebbles covered with a layer of mud and the principal companion plant

⁸ Sixth List of Additions to the Flora of Washington. *Loc. cit.*

is *Eriocaulon septangulare* With. The material collected at the Alexandria end of the bridge by Vasey and Coville, and Maxon's 1900 collection along with Steele's Anacostia material, soon to be mentioned, were made the basis of the new var. *reticulata* A. A. Eaton.

10. *Mount Vernon, Va.*, is on the west bank of the Potomac about 11^{km} south of Alexandria, Va. A specimen in the National Herbarium, collected at this place, bears the data: "Mt. Vernon, Va., July 4, 1889. Shore of the Potomac at the foot of the Mt. Vernon estate, Collector F. V. Coville." The collector describes (*in litt.*) the station as being "at the slope immediately in front of the house and therefore a hundred yards or more (100^m) north of the boat landing. There was a considerable area here in shallow water covered with *Isoetes*. The soil was gravelly."

11. *Notley Hall, Md.*, is on the east shore of the Potomac River, nearly opposite the mouth of Hunting Creek, Alexandria, Va. A specimen in the National Herbarium was collected at this place by F. V. Coville in 1894.

12. *Four Mile Run, Va.*—This creek enters the Potomac from the west about midway between Washington, D. C., and Alexandria, Va. Its lower course forms a wide bay, along the south side of which the banks are being eroded by wave action, which carries away the finer material, leaving a gently sloping tide-beach of mingled sand and gravel, on which *Isoetes* grows luxuriantly. The first collection at this station was made by E. S. Steele, August 5, 1898. The writer visited this place and made collections on August 22, 1902.

13. *Anacostia River* crosses the District of Columbia east of Washington, D. C., and empties into the Potomac River just south of that city. On September 1, 1900, E. S. Steele discovered *Isoetes* "on the southeast bank of the Anacostia River nearly opposite the Navy Yard, perhaps a half [one-fourth] mile below the Navy Yard bridge."⁹ This collection forms a part of the type material of var. *reticulata* A. A. Eaton.

14. *Sugar Loaf Creek* is a small stream which empties into Gunpowder River, western shore of Maryland, from the north,

⁹ In a letter to the writer.

at a point about 600^m northeast of Gunpowder station on the P. B. & W. R. R. On the small rounded point between Sugar Loaf Creek and Gunpowder River, I found *Isoetes saccharata* on September 2, 1902. The specimens were abundant but of small size, owing to the fact that they grew in a moderately dense colony of *Scirpus americanus* Pers., among which I have rarely found *Isoetes* elsewhere. Other associates of *Isoetes* at this station were *Lilaeopsis lineata* (Mx.) Greene, and *Eriocaulon septangulare* With. The soil conditions were typical—gravel covered with a thin layer of mud.

15. About 500^m above the mouth of Sugar Loaf Creek, on the east shore of Gunpowder River, I located another colony of *Isoetes* the following day, September 3, 1902. The specimens at this place were growing in a bed of sand only a few square meters in extent and were very thrifty.

16. *Havre de Grace Light* is on a small point on the west shore of the Susquehanna River at its mouth. The most interesting of T. C. Palmer's unpublished stations for *Isoetes* is a small area just north of this light house, near the pier. His collection at this point was made August 17, 1898, and is at present the northern known limit of the species.

17. *Havre de Grace Park* is along the shore of the bay, southwest of the Havre de Grace light. It descends to the bay by a steep bank, and below this bank, among the pebbles which pave the beach, I found the species growing abundantly, July 19, 1902.

18. Nearly 1^{km} west of the last, on the curved shore, known as the "knee" of the bay, *Isoetes saccharata* also grows, though not in such abundance as at the park station. I collected at this place also July 19, 1902, this being my first collection.

x. By this sign I have marked two points on Bush River at which single small specimens were found. The fact that these two specimens were seen indicates that its absence in notable quantity is due to unfavorable habitat, and not to barriers to its entrance. Although Bush River was explored from its mouth almost to the head of tide water, I did not see a single spot where I really expected to find it. The specimens found were evidently

choked by the density of the *Scirpus americanus* Pers., among which they grew. Where the shores were free from *Scirpus*, as they were for stretches north of Bush River station, P. B. & W. R. R., and at the mouth of Otter Creek, they were composed of pure gravel, subject to shifting with the action of the waves.

y. I have indicated thus the location of a well-grown specimen found floating in the bay at the mouth of Furnace Creek over 3^{km} from the nearest known colony.

It appears from this list of known stations that *Isoetes saccharata* has a general distribution in the fresh water portions of Chesapeake Bay and its tributaries, but is at present unknown from any other locality. If it has a wider distribution, our ignorance of that fact is not entirely due to lack of observation, for Delaware Bay, which furnishes the most accessible suitable habitats, has been explored by students of the genus, with the result that several stations have been located for *Isoetes riparia* Engelm., but not a single specimen of *I. saccharata* Engelm. has been found.

If the last named species is indeed limited to Chesapeake Bay, it will be of interest to consider the causes to which the restriction may be due. Endemic species have a peculiar interest in their bearing upon problems of biogeography. A cosmopolitan distribution is evidence of a high degree of adaptability to variation of habitat, and is also evidence either of an old species or of efficient means of dispersal. On the other hand, a species which is limited to a single locality is either a remnant of a once more widely distributed form, or it is a relatively new species which has arisen in the more or less isolated region to which it is now limited. In the first instance it has been protected by the barriers which surround it, or by peculiarly favorable conditions for its growth from the extinction which has overtaken the species in other regions; in the second case it has been prevented by barriers from spreading beyond the region of its origin. Cosmopolitan species seem to deny the existence of barriers, while local species not only confirm their existence but give a clue to the nature and position of these barriers. As biogeography has to do preeminently with barriers, it is evident

that species of local range are of the greatest importance in solving the fundamental problems of geographic distribution.

From this brief discussion it will be seen that there are two essentially different kinds of endemism. In one the species is a remnant, in the other it is a beginning. To the former of these the term *relict* endemism has been applied;¹⁰ to the latter I shall apply the term *initial* endemism.¹¹ Relict endemism is illustrated by such classic examples as the Sequoia of western North America and *Ginkgo biloba* L. of eastern Asia. Initial endemism is perhaps best exemplified by numerous endemic species of oceanic islands, though it does not follow that all endemic species of oceanic islands are initial.

It is obvious that many difficulties will be encountered in determining whether any local species in question is a relict or an autochthon. It is also obvious that we may have initial species of a relict genus, though not the reverse. After examining the nature of the barriers which limit the distribution of *Isoetes saccharata* I shall suggest to which class of endemic species it probably belongs.

It will have been noted in examining the map, or in looking over the descriptions of the several stations, that even within the narrow confines of Chesapeake Bay, this species is not generally distributed along the shores, but occurs only here and there in closely limited areas, the largest of which is perhaps less than 100^m long. This extreme localization within its range is due solely to the requirements of its habitat. The chief conditions necessary for its success are the following:

a) It is limited to tidal beaches, which fact restricts it to a narrow zone, never more than a few meters wide along the shore

b) It requires fresh water, never occurring in water of more than slight salinity. South of Spesutie Island the rivers have a

¹⁰ DRUDE, O., Handbuch der Pflanzengeographie 125. Stuttgart: J. Engelhorn. 1890.

¹¹ An initial species is called an autochthon and *autochthon* endemism might be used in contradistinction to *relict* endemism. Drude (*op. cit.* p. 124) refers to such species as "vicarious or corresponding forms," from which initial endemism is sometimes called *vicarious* endemism, but the significance of vicarious in this connection is too obscure to commend its adoption.

section near their mouths too salt for the growth of *Isoetes*, and this salt water section of the rivers becomes longer as we proceed toward the mouth of the bay. This isolates the suitable habitats in one river from those in neighboring rivers.

c) There must be sufficient stability of the soil of the shore to resist the action of the waves, and at the same time sufficient fineness of the soil particles to supply the needs of the plant without requiring an extensive root system. With one exception all the colonies visited by me grew on beaches characterized by rather coarse gravel set firmly in a matrix of sand, and covered over with a thin film of mud. The exception was found at my upper station on Gunpowder River, where a small but unusually luxuriant colony grew in a bed of sand. In this place the shore was protected from severe wave action by a zone of *Zizania aquatica* L., and I have no doubt that this circumstance alone made it possible for *Isoetes* to retain its hold at this place.

In Engelmann's manuscript notes, the following statement is accredited to William M. Canby: "I don't find any *Isoetes* (*riparia*, *Engelmanni*, *valida*, or *saccharata*) in pure mud or pure gravel; they always grow in mud which is deposited on gravel beds either by the tides (*riparia* and *saccharata*) or by rains which wash it down (*Engelmanni* and *valida*)."

d) *Isoetes saccharata* also requires that competition with other plants be slight. It is never found forming colonies of such density that it crowds itself, and its most frequent companion species have the same scattered habit. Only at my lower station on Gunpowder River have I found an exception to this. Here it is in competition with *Scirpus americanus* Pers. and is evidently suffering in the conflict. It would no doubt be entirely excluded by the *Scirpus* if the latter were as robust and densely set as is usual for that species on fresh water beaches.

When we consider the number of apparently essential elements in its habitat and the fewness and smallness of the areas in which all these elements are present, it is easy to understand the extreme localization of the species. But every restriction of habitat increases the difficulty of successful dispersal, and we may well ask how the species has succeeded in finding the places, often

so widely separated, which are adapted to its successful growth. Not only are difficulties presented by the requirements of its habitat, but there are factors in the life-history of *Isoetes saccharata* which are not favorable to rapid dissemination over wide areas. Heterospory is one of these. If spores are carried by any agency, microspores and megaspores must be lodged at the same place or the sporophyte itself must be carried. Besides, there seems to be a tendency in the species to dioecism,¹² and in proportion as this tendency is manifest the difficulties of dispersal are increased.

The means of dispersal upon which this and other species of like habitat may depend are several. The most important means must always be the water currents, because these are always acting at the time and place of spore production. Moreover, the chances are very good that the spores so carried may be lodged along some shore line where a new colony may be formed. In times of storm the waves may tear up whole plants from their anchorage in the littoral gravel and carry them far away to leave them finally stranded on some beach which may be adapted to the growth of the spores thus transported. Late last summer the writer saw a thrifty specimen of *Isoetes saccharata* floating in Chesapeake Bay, 100^m east of Stump's Point, at the mouth of Furnace Creek at the head of the bay, over 3^{km} from the nearest known station for the species, though possibly much nearer to some unknown station.

It is conceivable that biotic agencies might also occasionally serve as means of dispersal. Especially, from the observations of Charles Darwin and others, we might expect birds which frequent the shores to carry the spores occasionally on their feet or on their beaks, and as they move from one shore line to another, the spores so carried would be left in a new place favorable to growth. A. A. Eaton (*in litt.*) tells me that ducks are exceedingly fond of the spores of *Isoetes*, and that the lamellae of their beaks are especially fitted to retain them until washed

¹² PALMER, T. C., 1896, *loc. cit.* A. A. Eaton looks upon dioecism in this species as of rare occurrence, in which case it would be of slight importance in this connection.

out in another locality, and he thinks that this has been perhaps the efficient means of their dispersal.

A third possible method of dispersal is transportation of spores by the wind, but it is evident that successful dispersal by this means must be very rare. In the first place, the wind could only secure spores to carry after they had been stranded on the shore at high tide or in times of storm. Besides, the winds almost invariably blow across the shore line instead of parallel with it, so that the likelihood of the spores being stranded in a place adapted to their development is very slight indeed.

As the distribution of *Isoetes saccharata* appears to be limited by the confines of Chesapeake Bay, while the agency of birds and of the wind are not so limited, these agencies must be assumed to be relatively inefficient. For, if the waterfowl provided efficient means of dispersal, we should expect to find the species following the chief lines of migration as far as there were suitable habitats for its growth. As these lines of migration run parallel with the Atlantic coast, this would specially favor the transportation of *I. saccharata* into Delaware Bay and of *I. riparia* Engelm. into Chesapeake Bay. Our failure to find evidence of any such transportation is peculiarly striking when we bear in mind that the Back Creek station for *I. saccharata* is but little more than 16^{km} distant from the nearest point on Delaware Bay, while the known stations on Chesapeake Bay are in some instances separated by distances of more than 80^{km}.

We must conclude from these facts,¹³ I think, that water currents supply the only efficient means of dispersal for this species, and that these have supplied the means by which new colonies have sprung up in more or less distant areas. But even water currents could scarce be adequate to carry the spores from one

¹³This entire discussion is based on the assumption that *Isoetes saccharata* and *I. riparia* are really distinct species, as they have always been considered. In some of its forms *I. saccharata* approaches so nearly to *I. riparia* that the suggestion is not far that they are ecological varieties of the same species. Too little is known, as yet, about ecological varieties, to make more than a suggestion permissible. It is obvious that successful transportation from the one bay to the other may have taken place any number of times, if in each case the ecological conditions were such as to produce from the spores of a single specimen, *I. riparia* in Delaware Bay and *I. saccharata* in Chesapeake Bay.

station to the mouth of the river in which it occurs, thence up or down the coast to a neighboring river, and up that river to the fresh-water portion near the head of tide water. Such a transportation, if at all possible, must depend upon the most exceptional of circumstances.

Probably a truer explanation is found in relation to the geological history of the bay. It is believed by some geologists¹⁴ that the region about Chesapeake Bay is now sinking, and it is certain that it has recently sunk after a period of elevation. In fact, it seems to have been elevated and depressed several times in its Pleistocene history.¹⁵

The position of old shore lines with their sea cliffs and terraces gives evidence of the amount of subsidence of the land at each period of sinking, but no evidences remain as to the height to which the land rose during each period of elevation. The present elevation of the land is such that the water of the bay is fresh to Spesutie Island, about ten kilometers below the mouth of the Susquehanna River. During periods of greater elevation the water was fresh further to the south. When the land was so elevated that the water was fresh at the mouth of the Potomac River, favorable habitats along the shore of the bay must have been occupied by the progenitors of the *Isoetes saccharata* colonies which now occur in the upper estuarine portion of the tributary rivers. As the land sank and the rivers were ponded farther and farther from their mouths, new areas became adapted to the growth of *Isoetes*, and new colonies were formed. Simultaneously the colonies furthest down stream were destroyed by the advance of salt water. In this way there came to be, instead of a single colony or group of colonies at the head of Chesapeake Bay, as many distinct colonies as there were ponded tributaries. So long as the land continued to sink, the successful reproduction was on the up-stream side, and destruction followed *pari passu* on the down-stream side until the present condition of widely separated colonies was brought about. In periods of

¹⁴ COOK, GEORGE H., *Geology of N. J.* 1868: 343 *et seq.*

¹⁵ MCGEE, W J, *Am. Jour. Sci.* 35: 463-466. 1888. DARTON, N. H., *Bull. Geol. Soc. Am.* 2: 450. Ap 1891. SHATTUCK, GEORGE B., *Am. Geol.* 28: 100-105. Ag 1901.

elevation, the reverse process must have taken place, and the many distinct areas must have been merged again into one. This may have taken place as often as the bay has been up and down, and certainly has happened as often as the bay has risen and fallen since *Isoetes saccharata* entered it.

Just how or when *Isoetes* entered Chesapeake Bay is, of course, impossible to say, except that, according to this hypothesis of its dispersal, it must have been introduced before the last sinking of the coastal plain.

From what has been said of the requirements of its habitat and the means of dispersal of *Isoetes*, it will be seen that the barriers between Chesapeake Bay and Delaware Bay and between both of these and other fresh tidal waters, are of such definite character as to render these bays virtually islands of water in oceans of land. As we find *Isoetes saccharata* nowhere else than in Chesapeake Bay and *Isoetes riparia* nowhere else than in Delaware Bay, it seems fair to assume that neither of these species ever existed as such outside of the body of water to which it is now limited, and that we have here examples of initial endemism entirely comparable with that so common upon oceanic islands.

These two species are closely related and probably stand to each other in relation of parent and offspring; but which is the parent and which the offspring may not be easy to decide. Or perhaps they were the offspring of a common parent different from both. The nearness of this relationship was emphasized in the recognition of the two varieties, *Isoetes saccharata Palmeri* A. A. Eaton and *I. saccharata reticulata* A. A. Eaton, both possessing characters intermediate between *Isoetes saccharata* Engelm. and *Isoetes riparia* Engelm. The significance of these forms will be increased rather than lessened if they should prove to be untenable as varieties. For if these varieties are shown to be simply stages in the development of a polymorphic species, the greater range of variability which must then be admitted as a character of *I. saccharata* Engelm., coupled with the fact that those variations in several different features are in the direction of *Isoetes riparia* Engelm., would make almost certain the inference that an extreme variation of *I. saccharata* had become somewhat fixed through its isolation in Delaware Bay.

Careful cultures will be necessary to demonstrate conclusively the polymorphism of *Isoetes saccharata* Engelm., but that seems at present the most satisfactory explanation of the following facts. My attention was called both by A. A. Eaton and T. C. Palmer to several futile attempts which had been made to secure *typical* material from the *type* locality. It appears that the original description was written from a form which is of very rare occurrence. Even the co-type material did not agree with the type, and the Wicomico station has been visited several times since, but no typical material has been secured there. The infrequency of the recurrence of the typical form is well shown by the fact that my collection from Hunting Creek, Va., appears to be the first material collected since 1863, which agrees in its spore characters with the type material. The striking fact here is that my collection of typical *I. saccharata* Engelm. came from the type locality of variety *reticulata* A. A. Eaton. This colony is only a few square meters in extent and a considerable number of specimens had been collected there by Vasey and Coville in 1888, and by W. R. Maxon in 1900 and 1901. Every one of those specimens appear to have been var. *reticulata*. I collected at the same place perhaps a dozen specimens, every one of which was typical *I. saccharata*. The only plausible explanation of these facts, it seems to me, is that the identical plants which had been var. *reticulata* at the time of the previous collections, were last year typical *I. saccharata*.

Another similar circumstance which lends support to this explanation is that E. S. Steele's collection at Four Mile Run in 1899 was nearly typical *I. saccharata*, whereas the considerable number of specimens secured by me in 1902 from the same spot, all showed extremely well-marked characters of var. *reticulata* A. A. Eaton.

I have no such striking facts against the validity of var. *Palmeri* A. A. Eaton, since I visited no *Palmeri* station, but much of my material from the head of the bay was intermediate between *I. saccharata* and var. *Palmeri*, as was also Coville's Mount Vernon collection. T. C. Palmer found the same conditions at Cabin Johns Creek and Town Point in Elk River. If

Isoetes saccharata should prove to be polymorphic, as these facts suggest, the result will be of interest in its bearing upon such species as *I. echinospora* Durieu and *I. velata* A. Br., whose numerous intergrading forms have proved so baffling to systematists.

By way of summary, then, *Isoetes saccharata* Engelm. has been located in a number of tributaries of Chesapeake Bay from the the Potomac and Wicomico Rivers to the head of the bay.

The species is conceived to be autochthonous in Chesapeake Bay, and to bear toward *Isoetes riparia* Engelm. the relation of parent to offspring.

Its present distribution is explained by the geomorphic movements of the coastal plain.

Certain facts are presented which suggest that the species is polymorphic, and that the varieties *Palmeri* A. A. Eaton and *reticulata* A. A. Eaton are untenable.

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